

**Nomenclatural changes in *Chenopodium* (incl. *Rhagodia*)
(Chenopodiaceae), with considerations on relationships of some
Australian taxa and their possible Eurasian relatives**

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Abstract

Mosyakin, S.L. & Iamónico, D. Nomenclatural changes in *Chenopodium* (incl. *Rhagodia*) (Chenopodiaceae), with considerations on relationships of some Australian taxa and their possible Eurasian relatives. *Nuytsia* 28: 255–271 (2017). Following recent molecular phylogenetic results, species earlier placed in *Rhagodia* R.Br. were transferred to *Chenopodium* L. (Chenopodiaceae). However, three new species-level combinations proposed were later homonyms and thus illegitimate under ICN Art. 53.1. The new name *C. wilsonii* S.Fuentes, Borsch & Uotila [= *C. crassifolium* (R.Br.) S.Fuentes & Borsch, *comb. illeg.*] has been already proposed for one of these species. We propose here two new replacement names, *C. robertianum* Iamónico & Mosyakin, *nom. nov.* [≡ *R. hastata* R.Br. ≡ *C. hastatum* (R.Br.) S.Fuentes & Borsch, *comb. illeg.*] and *C. benthamii* Iamónico & Mosyakin, *nom. nov.* [≡ *R. crassifolia* R.Br. var. *latifolia* Benth. ≡ *C. latifolium* (Benth.) S.Fuentes & Borsch, *comb. illeg.*]. One new combination, *C. benthamii* subsp. *rectum* (Paul G.Wilson) Iamónico & Mosyakin, *comb. nov.* [≡ *R. latifolia* (Benth.) Paul G.Wilson subsp. *recta* Paul G.Wilson] is also validated. Indications of ‘holotypes’ of *R. hastata* by Scott and *R. crassifolia* var. *latifolia* by Wilson are corrected to lectotypes according to ICN Art. 9.9. Possible relationships and biogeographical links of Australian species earlier placed in *Rhagodia*, *Einadia* Raf., and Australian endemic groups of *Chenopodium* (sections *Auricoma* Aellen, *Desertorum* Paul G.Wilson, *Rhagodioides* Benth. etc.) with Eurasian taxa of *Chenopodium* (in particular, *C. sect. Acuminata* Ignatov, *C. frutescens* C.A.Mey., and newly recognised *C. sect. Vulvaria* (Standl.) Iamónico & Mosyakin, *comb. nov.*) are also discussed. Earlier predictions of these possible relationships are emphasised and new predictions are made, which should be tested by molecular phylogenetic and other methods.

Introduction

The family Chenopodiaceae (included in Amaranthaceae *s. lat.* according to APG 1999, APG II 2003, APG III 2009, APG IV 2016, but accepted as a distinct family in Hernández-Ledesma *et al.* 2015 and by nearly all experts in the group), as traditionally circumscribed, comprises 100–110 genera and approximately 1,600–1,700 species occurring in arid to semiarid, saline and disturbed habitats of temperate and subtropical regions, with a few representatives in the tropics (see e.g. Ulbrich 1934; Aellen 1960–1961; Kühn 1993; Hernández-Ledesma *et al.* 2015). The classification of this family and

the taxonomy of many groups within Chenopodiaceae were considerably changed, especially recently, following the progress of molecular phylogenetic studies (see Kadereit *et al.* 2003; Shepherd *et al.* 2004; Kadereit *et al.* 2005; Shepherd *et al.* 2005; Akhani *et al.* 2007; Cabrera *et al.* 2009; Kadereit *et al.* 2010; Cabrera *et al.* 2011; Kadereit & Freitag 2011; Fuentes-Bazan *et al.* 2012a; Fuentes-Bazan *et al.* 2012b; Kadereit *et al.* 2014; Walsh *et al.* 2015; Schüssler *et al.* 2016; Piirainen *et al.* 2017 etc.).

Among the critical groups of Chenopodiaceae, the phylogeny of *Chenopodium* L. *s. lat.* was only recently studied in detail by Fuentes-Bazan *et al.* (2012a, 2012b and references therein) who proposed a new classification scheme supporting some earlier phylogenetic results (e.g. Kadereit *et al.* 2003; Kadereit *et al.* 2005; Kadereit *et al.* 2010). Phylogenetically isolated positions of some segregate genera were confirmed in modified circumscriptions, e.g. *Blitum* L. (incl. *Monolepis* Schrad., *Scleroblitum* Ulbr.; see Fuentes-Bazan *et al.* 2012b, and compare to Scott 1978c) and *Dysphania* R.Br. (see Mosyakin & Clemants 2002; Clemants & Mosyakin 2003; Mosyakin & Clemants 2008; Shepherd & Wilson 2008, 2009; Fuentes-Bazan *et al.* 2012b etc.). Also, some long-forgotten genera were resurrected, such as *Lipandra* Moq., *Oxybasis* Kar. & Kir. and *Teloxys* Moq., and the new genus *Chenopodiastrum* S.Fuentes, Uotila & Borsch was proposed (Fuentes-Bazan *et al.* 2012b). The generic classification outlined in Fuentes-Bazan *et al.* (2012b) is now becoming almost universally accepted in many newer publications (e.g. Iamónico 2012; Mosyakin 2013; Uotila 2013; Sukhorukov *et al.* 2013; Iamónico 2014; Sukhorukov 2014; Sukhorukov & Kushunina 2014; Hernández-Ledesma *et al.* 2015).

On the other hand, some nomenclatural issues in *Chenopodium* still remain unresolved. Because of conflicting typifications of the genus [*C. album* L. vs *C. rubrum* L., now *Oxybasis rubra* (L.) S.Fuentes, Uotila & Borsch], a formal proposal to conserve this generic name with *C. album* as a conserved type has been made by Mosyakin (2015; see additional comments in Mosyakin *et al.* 2017). However, if the proposal by McNeill *et al.* (2016b) on selection of types of generic names using a largely mechanical method is accepted, for which there are very high chances (see also McNeill *et al.* 2016a; Turland & Wiersema 2017), the typification of *Chenopodium* with *C. rubrum* (Britton & Brown 1913; Standley 1916) will be superseded and *C. album* will be the non-supersedable type of the genus, regardless of any decision on the *Chenopodium* conservation proposal (Mosyakin 2015).

***Rhagodia*, *Einadia* and *Chenopodium*: an overview of possible relationships**

Historical studies

The Australian genera *Rhagodia* R.Br. and *Einadia* Raf. (sometimes merged into a single genus under the priority name *Rhagodia*) were segregated by Scott (1978a), together with South American *Holmbergia* Hicken, in a separate subtribe Rhagodiinae A.J.Scott. However, Kadereit *et al.* (2010) demonstrated that *Holmbergia* should be placed in the tribe Atripliceae Duby within the *Archiatriplex* G.L.Chu clade, where its position remained unresolved. Kadereit *et al.* (2010) commented, however, that '[m]orphologically, *Holmbergia* does not show particular similarities to any of the other genera of the *Archiatriplex* clade' and also mentioned that, despite having superficially similar fleshy or coloured fruits, *Holmbergia* and *Rhagodia* are profoundly different in their pericarp anatomy. In fact, 'the 3–5(6)-layered, undifferentiated pericarp of *Holmbergia* is dry, and the reddish appearance of the fruit is caused by the hard, dark red-brown testa' (Kadereit *et al.* 2010: 1672; see also Sukhorukov 2014). Thus, *Holmbergia* is excluded from our further discussion.

The uncertainty of delimitation between *Chenopodium*, *Rhagodia* and *Einadia* was already recognised by botanists of the 19th Century. In fact, the similarity between *Chenopodium* and *Rhagodia* was

noted by Brown (1810: 408), who provided the following observation in the protologue of his newly described genus: 'Obs. *Chenopodio proxima*; Fructu baccato floribusque polygamis diversa'. Bentham commented in reference to *Rhagodia* '[t]his genus is exclusively Australian, differing from *Chenopodium* in the succulent pericarp and usually in the more shrubby habit' (Bentham 1870: 152); however, when discussing *Chenopodium* he stated that '[t]he precise limits to be assigned to the genus are as yet very uncertain' (Bentham 1870: 157). The translation from German of Diels and Pritzel (1905: 179) reads: 'The genus *Rhagodia*, which is widely represented in Western Australia, is only slightly different from *Chenopodium*. Several species assigned to it are still unknown with their fruits and therefore cannot be classified with certainty'. Aellen (1939, 1960–1961, 1964) included taxa of *Einadia* in *Chenopodium* and placed them in his *C. sect. Polygonoidea* Aellen.

Wilson (1987) in his important but rarely cited article proposed a scheme based on morphological evidence where *Rhagodia* was placed as sister to *C. sect. Desertorum* Paul G. Wilson, *Einadia* was considered to be close to *C. sect. Leprophyllum* Dumort. (now *sect. Chenopodium*, if *C. album* is accepted as the lectotype of the genus), and *C. sect. Rhagodioides* Benth. was placed between these two groups. In his earlier publications Wilson (1983, 1984) also emphasised possible links between the mentioned groups. He considered possible taxonomic solutions and concluded that 'a nomenclature that reflects a more natural classification of the Australian "mealy" members of the *Chenopodium* complex is required but it is unclear as to whether this is better achieved by raising the various sections to generic rank or whether the circumscription of *Chenopodium* should be expanded to encompass genera such as *Einadia* and *Rhagodia*. This matter is difficult to resolve in isolation since a number of extra-Australian sections and genera are involved' (Wilson 1987: 80). The close evolutionary links between these Australian genera and corresponding sections of *Chenopodium* were also discussed by Mosyakin (2003a, 2003b, and references therein). Furthermore, uncertain circumscriptions of *Chenopodium*, *Einadia* and *Rhagodia* are also evident from the synonymy of Australian species, where some recognised taxa often have synonymic names and combinations available in all three genera (Wilson 1983, 1984, 1987; Council of Heads of Australasian Herbaria 2005–; IPNI 2012).

Reliability of morphological characters

Fleshy fruits or infructescences occur in some species belonging to several genera of Chenopodiaceae, e.g. *Chenopodium* (incl. *Rhagodia*), *Blitum*, *Suaeda* Forssk. ex J.F.Gmel., *Anabasis* L., *Enchylaena* R.Br., and some others (Ulbrich 1934; Wilson 1984; Kühn 1993; Mosyakin 2003b; Sukhorukov & Zhang 2013; Sukhorukov 2014); the modified parts becoming fleshy (succulent) at the fruiting stage are mainly perianth segments (tepals) or the pericarp. Thus, the inclusion of fleshy-fruited taxa of *Rhagodia* and *Einadia* in *Chenopodium* should not be seen as a great surprise. As noted by Kadereit *et al.* (2010: 1672): 'Berry-like fruits evolved several times in Chenopodiaceae in rather isolated positions. This character state does not seem to be phylogenetically informative in the family'. Dinan *et al.* (1998: 572), after studying phytoecdysteroids of selected taxa of Chenopodiaceae, emphasised 'the close association between *Einadia* and *Rhagodia* with *Chenopodium* subgenus *Chenopodium*, especially sections *Polygonoidea* and *Desertorum*, respectively'. Thus, close links of *Rhagodia* and taxa of *Chenopodium* are confirmed by evidence from carpology (Sukhorukov & Zhang 2013; Sukhorukov 2014) and biochemistry (Dinan *et al.* 1998).

As it has been demonstrated by recent molecular studies (Kadereit *et al.* 2003; Kadereit *et al.* 2010; Kadereit & Freitag 2011; Fuentes-Bazan *et al.* 2012b etc.) and suggested by many earlier authors (e.g., Ulbrich 1934; Wilson 1987; Kühn 1993, among others), in Chenopodiaceae (as well as in many other taxonomically complicated groups of plants) some easily observable and eye-catching characters that were used in pre-molecular taxonomy as diagnostic features for distinguishing genera are often

misleading, and especially for phylogenetic inferences. This is evident in the tribe Camphorosmeae Moq. (including Sclerolaeneae A.J.Scott and Maireaneae A.J.Scott) (see Wilson 1987; Cabrera *et al.* 2009, 2011; Kadereit & Freitag 2011; Kadereit *et al.* 2014; and compare with Scott 1978b), as genera therein were traditionally delimited mainly on the presence and/or shape of appendages on fruiting perianth segments (wings, spines, hooked or winged spines, tubercles etc.) and some other rather evident characters. However, new studies showed that similar appendages can be present in different and phylogenetically distant clades, while morphologically very different appendages may occur in one clade. It is especially true for Australian taxa of Camphorosmeae (earlier sometimes segregated in a separate tribe or even two tribes, see above), in which the limits and circumscriptions of many genera still remain obscure (Cabrera *et al.* 2009, 2011). No satisfactory generic rearrangement in that group has been proposed so far. Evidently, search for alternative and often not so evident diagnostic characters (including anatomical and micromorphological ones) is needed in that and many other groups of Chenopodiaceae to achieve reliable and morphologically supported genus-level classification.

Phylogenetic studies

Recent molecular phylogenetic studies of *Chenopodium* and its relatives have unfortunately included only a few species of Australian endemic taxa of *Chenopodium*, *Rhagodia* and *Einadia*. While these studies in general confirmed the close links of *Rhagodia* and *Einadia* with *Chenopodium s. str.*, the nature of these links remained largely unresolved. For example, Kadereit *et al.* (2003) included in their analysis *C. auricomum* Lindl., *C. desertorum* (J.Black) J.Black and *R. drummondii* Moq., and reported that these three Australian species appeared ‘in a well-supported subclade (78% bootstrap) sister to the taxa from Eurasia and Juan Fernandez Islands’ (Kadereit *et al.* 2003: 976). The non-Australian species included were Eurasian *C. acuminatum* Willd. and *C. frutescens* C.A.Mey., and Juan Fernándezian *C. sanctae-clarae* Johow, which was hardly a representative sampling for such a widespread and diverse group containing numerous Eurasian, American and African taxa. Despite that, this important pioneering molecular phylogenetic study has already demonstrated (1) the position of a *Rhagodia* in a clade with the two other Australian species and within the larger clade of Chenopodieae I (containing the ‘typical’ taxa of *Chenopodium*), and (2) the fundamental divergence between Chenopodieae I, Chenopodieae II (containing *Blitum*, *Spinacia* L. etc.), and Chenopodieae III (containing *Dysphania* in a narrow sense, ‘glandular’ species of *Chenopodium s. lat.*, etc.). These data for the first time convincingly confirmed the predictions regarding the profound split between ‘mealy’ and ‘glandular’ taxa made by earlier authors (Carolin 1983; Wilson 1983, 1987; Mosyakin & Clemants 2002). For example, Wilson’s (1987) ‘glandular’ taxa (*Dysphania s. str.*, *C. sect. Orthosporum* R.Br. and ‘*C. sect. Ambrina*’) were placed in a clade opposite to another clade of ‘mealy’ taxa having vesicular trichomes (incl. *Scleroblitum*, *Chenopodium*, *Einadia*, *Rhagodia* and *Atriplex* L.). The links between Australian taxa usually placed in *Dysphania* and *C. sect. Orthosporum* were also discussed earlier by Aellen (1930a, 1930b, 1933), who, however, preferred at that time to subsume *Dysphania* under *Chenopodium*.

Kadereit *et al.* (2005) confirmed the findings reported in Kadereit *et al.* (2003) and hypothesised that ‘*Chenopodium* subg. *Chenopodium/Rhagodia* (4.7–2.9 Mya) both arrived [to Australia] during the Pliocene’; at the same time they recognised that ‘[t]he geographic origin of the *Chenopodium* subg. *Chenopodium/Rhagodia* clade, and its mode of entering Australia, are unclear and needs further extended sampling’ (Kadereit *et al.* 2005: 77). In an expanded study Kadereit *et al.* (2010) placed *Rhagodia* (with *R. drummondii* and *R. parabolica* R.Br. sampled) and *Einadia* (with *E. nutans* (R.Br.) A.J.Scott sampled) in a subclade including Australian *C. auricomum*, *C. desertorum* and *C. nitrariaceum* (F.Muell.) Benth. within the Chenopodieae *s. str.* (Chenopodieae I) clade.

Fuentes-Bazan *et al.* (2012a, 2012b) included in their analysis *E. nutans* (*C. nutans* (R.Br.) S.Fuentes & Borsch) and *R. triandra* (G.Forst.) Aellen (*C. triandrum* G.Forst.) and confirmed that *Rhagodia* and *Einadia* are phylogenetically rooted in *Chenopodium s. str.* However, because only a few Australasian species were included in the analyses of Kadereit *et al.* (2003, 2005, 2010) and Fuentes-Bazan *et al.* (2012a, 2012b), the phylogenetic resolution for these taxa remained insufficient (see below). In our opinion, key Eurasian taxa of *Chenopodium* that may possibly be related to Australian taxa were also not sampled in Fuentes-Bazan *et al.* (2012a, 2012b).

The new important findings that resulted from the molecular phylogenetic study by Walsh *et al.* (2015) are discussed below.

Considerations on relationships of some Australian taxa of *Chenopodium* (incl. *Rhagodia*) and their possible Eurasian relatives

As we mentioned above, close links between *Rhagodia*, *Einadia* and some Australian taxa usually placed in *Chenopodium* were noted and discussed by several authors well before the advent of molecular phylogenetic methods. These suggestions were confirmed by recent molecular studies. However, we were unaware of earlier hypotheses directly linking Australian endemic taxa of *Chenopodium s. lat.* with their possible Eurasian relatives, except for some rather general assumptions.

The possible links of Australian endemic taxa to Eurasian annual *C. vulvaria* L. and subshrubby *C. frutescens* (both species having the peculiar trimethylamine smell, often described as that of ‘rotten fish’) were already suggested and considered by Mosyakin (2003b: 216), who provided the following discussion (in Ukrainian, here given in English translation): ‘The exclusively Australian sections *Polygonoidea* Aellen (1964, Feddes Repert. sp. nov. 69: 69) and *Desertorum* P.G. Wilson (1983, Nuytsia 4(2): 151) are not discussed here in detail because at present there is not enough data on their relationships and taxonomic peculiarities sufficient for a reliable phytogeographic analysis. It should be noted, however, that species of sect. *Desertorum*, despite their morphological features (for example, tendency to form fleshy fruits, similar to those in the genus *Rhagodia*), are evidently close to Eurasian species related to *C. vulvaria* and *C. frutescens* (see also discussion of subsect. *Chenopodium*). Thus, most probably, sect. *Desertorum* can be regarded as a result of ancient migration of ancestral Asian species due to a long-distance dispersal event and their further adaptive evolution under specific conditions of arid interior regions of Australia’.

It should also be stated that *C. frutescens* can be viewed as a morphological link between *C. vulvaria*, with which it shares the trimethylamine smell and similar leaf shape, and the group of *C. acuminatum* (sect. *Acuminata* Ignatov) in regards to the similar leaf shape and structure, and the linear inflorescences. The trimethylamine smell seems to occur mainly in early-branching clades of *Chenopodium*; however, several other Australasian, Eurasian and American taxa also have the same or similar odour (but usually not as strong as in *C. vulvaria*, sometimes barely perceptible) and because of that the phylogenetic importance of that biochemical character remains obscure.

Mosyakin (2003a, 2003b) also discussed possible links between taxa of *C. sect. Auricomma* Aellen and sect. *Acuminata*: ‘The Australian section *Auricomma* Aellen, which is represented by two endemic Australian species, shrubby *C. auricomum* and annual *C. auricomiforme* Murr & Thell., is characterised by both vesicular farinose and tubular multicellular trichomes, which are located mainly on branches of inflorescences (Carolin 1983; Wilson 1983, 1984). The presence of this rare character, as well as narrowly elliptic, ovate or slightly trilobate leaves with semitranslucent margins, indicates that sect.

Auricoma is to some extent related to sect. *Acuminata*. The latter (section) is represented in Asia by *C. acuminatum* and its close relative *C. vachellii* Hook. & Arn. Thus, these two groups (sections) form together an Australasian type of distribution, which is reasonable from the phytogeographical viewpoint. However, the phytogeographic and phylogenetic significance of these links still remains insufficiently explained. We can logically assume migration scenarios of Asian taxa southward or of Australian taxa northward. In my opinion, the first scenario is more realistic. As it has been emphasised by P.G. Wilson (Wilson 1983), the Australian section is very similar to sect. *Chenopodium* (which was reported by Wilson under the erroneous name, as sect. *Leprophyllum* s. lat., including almost all subdivisions of subgen. *Chenopodium*), especially if sect. *Auricoma* includes *C. auricomiforme*, which is a connective link between these two groups.

In my [SLM] opinion, '*C. auricomiforme*, which occurs in the eastern part of Australia (SE Queensland and NE New South Wales), is indeed transitional, but toward sect. *Acuminata*, not to sect. *Chenopodium*. Its distribution in Australia is also noteworthy. This species does not occur in extreme arid regions of Australia, where *C. auricomum* occurs. A similar situation is observed also in Asia, where typical *C. acuminatum* is widespread in continental arid habitats from Central Asia to the south-easternmost Europe, mainly within the Irano-Turanian region in a wide sense, while *C. vachellii* is a species of more humid regions and often littoral habitats of Eastern and South-eastern Asia. We can assume that littoral Asian species in the past migrated to Australia, and the shrubby habit evolved in plants of that group during their isolation and colonisation of the inner parts of the island continent as an adaptation in response to arid habitat conditions' (translated from Ukrainian: Mosyakin 2003a: 27; see also further details in Mosyakin 2003b: 218–220). Mosyakin (in Zhu *et al.* 2003: 380) also commented that 'judging from the presence of characteristic multicellular hairs (especially in the inflorescence) and leaf and inflorescence morphology, *C. acuminatum* s.l. (*C.* sect. *Acuminata* Ignatov) is related to the Asian perennial *C. fruticosum* [a typo – should be *C. frutescens*] C.A.Meyer, the Australian shrubby *C. auricomum* Lindley (the latter, together with the annual *C. auricomiforme* Murr, is placed in *C.* sect. *Auricoma* Aellen), and probably to some other shrubby species'.

The peculiar linear multicellular trichomes present on inflorescence branches of the Australian and Asian taxa seem to be an important morphological synapomorphy of sections *Acuminata* and *Auricoma*. This character was observed in Australian *C. auricomum* and *C. auricomiforme* (Aellen 1960–1961: 572; Wilson 1983, 1984) and Eurasian *C. acuminatum* (Aellen 1960–1961: 572) and *C. vachellii* (Iljin & Aellen 1936: 59). These trichomes were termed 'tubular hairs' by Aellen (1960–1961: 572; 'Schlauchhaare' in German), 'contorted tubular multi-cellular hairs' by Wilson (1983: 138), and 'sausage-like hairs' ('колбасовидные волоски' in Russian) by Iljin and Aellen (1936: 59) and Ignatov (1988: 18–19).

Mosyakin (2003a, 2003b) was not the first who noted the close similarity between *C. auricomum* and *C. acuminatum*. Bentham (1870: 159) provided the following comment under *C. auricomum*: 'This species undoubtedly comes near to some forms of *C. album*, differing in its entire more tomentose leaves and larger flowers. It appears to be still more closely allied to and perhaps not really distinct from the East Asiatic *C. acuminatum*, Willd.' Of course, the shrubby Australian *C. auricomum* is definitely not conspecific with annual *C. acuminatum* (and also not close to *C. album*), but that note was probably explained by the fact that Bentham had at his disposal only limited material of both these species. Wilson (1983, 1984) rejected Bentham's suggestion of conspecificity of *C. auricomum* and *C. acuminatum* but refrained from proposing any concept of their possible relationships.

A new molecular phylogenetic study (Walsh *et al.* 2015) brought additional noteworthy conclusions involving Australian taxa; these conclusions are important for our further discussion and deserve to

be cited here in full:

‘The ‘Vulvaria & Auricomum’ clade is sister to the rest of *Chenopodium* and consists of *C. vulvaria* (European, but currently widely dispersed) and *C. auricomum* (Australian). Resolution of the basal nodes within the *Chenopodium* clade are fully congruent with, yet better resolved than, the results observed in previous analyses that used ITS and plastid sequence data (Fuentes-Bazán *et al.*, 2012a, b). That is, our phylogenetic results support the recent taxonomic segregation of parts of *Chenopodium* s.l. into other genera. One difference, however, is that there is strong support in our *SOSI* results linking *C. vulvaria* and *C. auricomum* in a clade that is the sister group of a clade comprising all other members of *Chenopodium* s.s. Several previous studies using plastid markers (Kadereit *et al.*, 2003, 2005, 2010) found that Australian and New Zealand *Chenopodium*, including *C. auricomum*, group together in a clade with species of *Rhagodia* R.Br. and *Einadia* Raf., to the exclusion of *Chenopodium* species from other continents. The ITS sequence data of Fuentes-Bazán *et al.* (2012a, b), on the other hand, found that *Rhagodia* and *Einadia* did not group in a clade, but were unresolved within a clade otherwise composed of *Chenopodium* (core-*Chenopodium* clade), itself sister to *C. vulvaria*. Based solely on the ITS phylogeny, a taxonomic revision was proposed subsuming *Rhagodia* and *Einadia* into *Chenopodium* to make *Chenopodium* monophyletic (Fuentes-Bazán *et al.*, 2012a). Our results suggest an alternative relationship among the Australian genera and *Chenopodium*. That is, if *C. auricomum* is indeed representative of the broader Australian–New Zealand clade, we predict that if *Rhagodia* and *Einadia* species were included in this analysis, they would form an entirely Australian–New Zealand clade with *C. auricomum*, sister to *C. vulvaria*, together forming a distinct clade sister to the remaining *Chenopodium* s.s. species. We suggest that more studies are needed to determine whether subsuming *Rhagodia* and *Einadia* into *Chenopodium* is appropriate. If *Rhagodia* and *Einadia* are indeed embedded within *Chenopodium* s.s., this will have interesting implications, because *Rhagodia* and *Einadia* differ from *Chenopodium* in having fruit in the form of fleshy berries, perennial shrub habit, and unisexual flowers (Brown, 1810)’ (Walsh *et al.* 2015: 541).

In our opinion, the recognition of the early-branched clade (or clades?) of *Chenopodium* as a separate genus (most probably under the priority name *Rhagodia*), as it was cautiously suggested by Walsh *et al.* (2015) as one of possible solutions, is hardly justified, especially considering the close links between the Australian and Eurasian taxa and their morphological similarities (see above). Most probably several subgroups/subclades corresponding to re-circumscribed sections will be revealed within the lineage currently informally called the ‘Vulvaria & Auricomum’ clade (Walsh *et al.* 2015).

Chenopodium acuminatum and *C. vachellii* (‘*C. virgatum*’ *auct. p.p., non* Thunb.) are currently included in *C. sect. Acuminata* (Ignatov 1988; Mosyakin 1996, 2003a); however, supposedly related Australian taxa were placed in several (at least three) sections of *Chenopodium* and in two segregate genera (Wilson 1983, 1984). No formal taxonomic placement in any infrageneric taxon outside of *C. sect. Chenopodium* was proposed by anyone for the phylogenetically important group of *C. vulvaria* (including *C. rhombicum* (Murr) F.Dvořák, *C. nidorosum* Otschiauri, and some other taxa, which are hardly specifically different from it) and its few possible Eurasian relatives. Mosyakin (2003a: 29) noted earlier that *C. vulvaria* and the supposedly closely related group of poorly known (and most probably relict) mountain species from Asia require special attention and formal taxonomic recognition, probably as a separate subsection (or two subsections). Standley (1916) had earlier segregated *C. vulvaria* (together with two American species) in an unranked infrageneric group, which is validly published but inoperative in questions of priority except for homonymy; it can be used as a basionym or replaced synonym for subsequent new combinations, names at new ranks, or replacement names in definite ranks (*ICN* Art. 37.3: McNeill *et al.* 2012). This group can be now formally recognised as a section, which is validated below.

It should be noted that the North American taxa *C. watsonii* A. Nelson and *C. parryi* Standl., which Standley (1916) also placed in his ‘*Vulvariae*’ group, should be excluded from it because they are not closely related to *C. vulvaria*, judging from morphological, biogeographical (Mosyakin & Clemants 1996; Clemants & Mosyakin 2003, and references therein), and now also molecular phylogenetic (Walsh *et al.* 2015) evidence. In particular, Mosyakin and Clemants (1996: 401) placed *C. watsonii* s. lat. in *C.* sect. *Chenopodium* subsect. *Favosa* (Aellen) Mosyakin & Clemants but also indicated that this species aggregate, ‘evidently being related to *C. berlandieri*, at the same time closely approaches morphologically some forms of the *C. fremontii* aggregate, and possibly may be included together with the latter in *Chenopodium* subsect. *Fremontiana*’. Walsh *et al.* (2015) revealed the diploid *C. watsonii* in the mainly American ‘Genome A’ clade containing, for example, North American diploids *C. standleyanum* Aellen, *C. fremontii* S. Watson, *C. leptophyllum* (Moq.) Nutt. ex S. Watson (with only ‘A-genome’ homeologs), tetraploid *C. berlandieri* Moq. (having also ‘B-genome’ homeologs), and South American tetraploids *C. quinoa* Willd. and *C. hircinum* Schrad. (also combining in their genome A and B homeologs) etc., but also East Asian diploid *C. bryoniifolium* Bunge and probably some other Asian taxa, although relationships within this clade remain poorly resolved.

We prefer here to leave *C. frutescens* yet unplaced in any section because of its characters being transitional between those of members of the *Acuminata* and *Vulvaria* groups. Morphology indicates that *C. frutescens* is probably closer to *C. acuminatum*, having similar leaves and inflorescences, but since easily observable morphological traits in Chenopodiaceae can be misleading (see above), we should wait for solid molecular evidence. The same is true for other supposed Asian relatives of *C. vulvaria*; they may represent other early-branching lineages not yet revealed in the available molecular phylogenetic studies.

Taxonomy

After confirming phylogenetically rooted positions of taxa of *Rhagodia* and *Einadia* within the clade of *Chenopodium* s. str., Fuentes-Bazan *et al.* (2012a) made nomenclatural transfers of species of these two Australian genera to *Chenopodium*. When doing that, they coined three illegitimate combinations which are later homonyms of earlier names (ICN Art. 53.1: McNeill *et al.* 2012). One of those illegitimate combinations, *C. crassifolium* (R.Br.) S. Fuentes & Borsch, *comb. illeg.*, was soon noticed and the new replacement name *C. wilsonii* S. Fuentes, Borsch & Uotila has been published (Fuentes-Bazan *et al.* 2012b).

For two other combinations, *C. hastatum* (R.Br.) S. Fuentes & Borsch, *comb. illeg.* and *C. latifolium* (Benth.) S. Fuentes & Borsch, *comb. illeg.*, there are no correct names under *Chenopodium* currently available. As such, we propose here new names for these species.

The herbarium acronyms are given following *Index Herbariorum* (Thiers continuously updated). Online images of types and other specimens were consulted using *Global Plants* (<https://plants.jstor.org>) and online resources of corresponding herbaria.

Chenopodium robertianum* Iamónico & Mosyakin, *nom. nov.

Rhagodia hastata R.Br., *Prodr. Fl. Nov. Holland.*: 408 (1810). ≡ *Einadia hastata* (R.Br.) A.J. Scott, *Feddes Repert.* 89: 4 (1978). ≡ *Chenopodium hastatum* (R.Br.) S. Fuentes & Borsch, *Molec. Phylogen. Evol.* 62: 372 (2012) (as ‘*hastata*’), *comb. illeg.*, *non C. hastatum* Phil., *Fl. Atacam.*: 47 (1860); *nec C. hastatum* Dumort., *Bull. Soc. Roy. Bot. Belgique* 4: 339 (1865), *nom. illeg.*; *nec C. hastatum* St.-Lag., *Étude Fl.*, ed. 8 [A. Cariot] 2: 703 (1889), *nom. illeg.*; *nec C. hastatum* (C. Klinggr.) Murr, *Magyar*

Bot. Lapok 1: 360 (1902), *nom. illeg.* *Type*: Port Jackson, New South Wales, Australia, *R. Brown s.n.* [Bennett No. 3040] (*lectotype fide* A.J. Scott, *Feddes Repert.* 89: 4 (1978): BM 001010211 image seen; *isolectotypes*: BM 001015889 image seen, K 000898399 [plant of the bottom-half of the sheet] image seen, MEL 545196 image seen).

Etymology. The newly proposed epithet commemorates Robert Brown (1773–1858), an outstanding British botanist and pioneer of Australian plant taxonomy, who authored the replaced name. We prefer not to use the epithet ‘*brownii*’ because of the existing name *C. brownianum* Schult. (published as ‘*browneanum*’, a replacement name for *C. lanceolatum* R.Br. 1810, *nom. illeg., non* Willd. 1808), following *ICN* Art. 23, Rec. 23A.2 (McNeill *et al.* 2012), according to which the use of the genitive and the adjectival form of the same word to designate two different species of the same genus should be avoided.

Notes on typification. In the protologue, Brown (1810: 408) indicated that he observed living plants at Port Jackson *via* the citation ‘(J.) v. v.’ (meaning ‘Port Jackson, *vidi vivo*’) but did not cite any particular specimen that can be regarded as the holotype (as defined by *ICN* Art. 9.1: McNeill *et al.* 2012). Scott’s (1978a: 4) reference to the specimen from Brown’s own herbarium with a Bennett number of 3040 (BM 001010211) as the ‘holotype’ is an error to be corrected to ‘lectotype’ according to *ICN* Art. 9.9 (McNeill *et al.* 2012).

Chenopodium benthamii* Iamónico & Mosyakin, *nom. nov.

Rhagodia crassifolia R.Br. var. *latifolia* Benth., *Fl. Austral.* 5: 155 (1870). ≡ *Rhagodia latifolia* (Benth.) Paul G. Wilson, *Nuytsia* 4(2): 228 (1983). ≡ *Chenopodium latifolium* (Benth.) S.Fuentes & Borsch, *Molec. Phylogen. Evol.* 62: 372 (2012), *nom. illeg., non* *C. latifolium* (Wahlenb.) E.H.L.Krause in Sturm, *Deutschl. Fl.*, ed. 2, 5: 174 (1901). *Type*: Dirk Hartog Island, Western Australia, Australia, [21–25 January 1822], A. Cunningham 321 (*lectotype fide* P.G. Wilson, *Nuytsia* 4: 228 (1983): K 000898390 image seen; *isolectotypes*: K 000898393 image seen; MEL 545194 image seen).

Etymology. The newly proposed epithet commemorates George Bentham (1800–1884), an outstanding British botanist and the author of the replaced name.

Notes on typification. Bentham (1870: 155) proposed his new var. *latifolia* to distinguish forms of *R. crassifolia* growing on Dirk Hartog Island, which were characterised by having ‘leaves obovate ovate hastate or broadly oblong, all very obtuse and under ½ in. long’. Bentham (1870) also cited ‘*R. crassifolia*, Moq. in DC. Prodr. xiii. ii. 52’ and the collector ‘A. Cunningham’. This citation should be viewed as the direct reference to the updated description by Moquin-Tandon (1849: 52), who accepted Brown’s species name and reported ‘Cunningh.!’ as one of its collectors. Most probably Moquin-Tandon studied in de Candolle’s herbarium (‘v. s. in h. DC.’, meaning G-DC) only the specimen collected by Cunningham (as indicated by the exclamation point) and based his updated description on that specimen. Consequently, Bentham (1870) probably intended to consider Moquin-Tandon’s concept of *R. crassifolia* (as opposed to the original understanding of the species by Brown) as applicable to his new var. *latifolia*.

Allan Cunningham visited Dirk Hartog Island from 21 to 25 January 1822 (Heward 1842: 274–275), and thus all his specimens from that locality were collected during this period. We have traced three germane specimens (K 000898390, K 000898393 [plant on the bottom-half of the sheet]) and MEL 545194, only one of which (K 000898390) reports the collection date (‘*Jan* 1822’). Scott (1978a: 9) cited the

type as ‘Cunningham 321 (K-holo.!)’. Since there are at least two such specimens at K, this should be regarded as a first-step lectotypification. However, Wilson (1983: 228) cited the dated specimen from K as ‘Dirk Hartog Is., Jan. 1822, A. Cunningham 321 (holo: K; iso: MEL)’. By doing that, he explicitly identified this dated specimen as the type, thus in fact providing the second-step lectotypification. His type designation (‘holotype’) is correctable to lectotype under *ICN* Art. 9.9 (McNeill *et al.* 2012).

Chenopodium benthamii subsp. **rectum** (Paul G. Wilson) Iamónico & Mosyakin, *comb. nov.*

Rhagodia latifolia (Benth.) Paul G. Wilson subsp. *recta* Paul G. Wilson, *Nytsia* 4(2): 228 (1983).
 ≡ *Chenopodium latifolium* (Benth.) S. Fuentes & Borsch subsp. *rectum* (Paul G. Wilson) S. Fuentes & Borsch, *Molec. Phylogen. Evol.* 62(1): 372 (2012). *Type*: Victoria District, Geraldton [Western Australia], January 1901, *Diels & Pritzel* 542 [as 212] (*holotype*: PERTH 01567128 image seen).

Updated citations of infrageneric taxa and validation of a new section

The names of infrageneric entities *Auricoma* and *Acuminata*, here recognised as sections, were initially published invalidly and because of that they were sometimes cited with incorrect places of their valid publication, and incorrect ranks and authorship. For that reason we provide below their updated nomenclatural citations.

Chenopodium sect. **Acuminata** Ignatov, *Sosud. Rast. Sovet. Dal'nego Vostoka [Pl. Vasc. Orient. Extrem. Sov.]* 3: 18 (1988). *Chenopodium* sect. *Chenopodia* C.A. Mey. ser. *Acuminata* Aellen & Iljin, *Fl. URSS* 6: 56 (1936), *nom. inval., descr. ross.*; *Chenopodium* sect. *Chenopodium* subsect. *Acuminata* Aellen in Hegi, *Ill. Fl. Mitt.-Eur.*, 2nd edn, 3(2): 578 (1961), *nom. inval., descr. germ.*

Type: *C. acuminatum* Willd.

Species: *C. acuminatum* Willd., *C. vachellii* Hook. & Arn. (*C. acuminatum* var. *vachellii* (Hook. & Arn.) Moq., *C. tonkinense* Courchet, *C. virgatum* auct. non Thunb.; *C. acuminatum* subsp. *virgatum* auct. non (Thunb.) Kitam.); probably also *C. frutescens* C.A. Mey. (now unplaced in any section pending further research; see discussion above).

The application of the name *C. virgatum* Thunb. (not *C. virgatum* (L.) Ambrosi, *nom. illeg.* = *Blitum virgatum* L.) remains problematic. Zhu *et al.* (2003: 380) noted that ‘there was much controversy regarding the taxonomic affiliation of *C. virgatum*: some authors believed that the name refers to narrow-leaved forms of the *C. album* aggregate or to *C. strictum*’. We follow here the concept of *C. virgatum* as accepted by Aellen (1960–1961), Uotila (2001), and some other authors, who considered this taxon a member of the *C. album* aggregate.

Chenopodium sect. **Auricoma** Aellen, *Feddes Repert.* 69: 69 (1964). Aellen in Hegi, *Ill. Fl. Mitt.-Eur.*, 2nd edn, 3(2): 577 (1961), *nom. inval., descr. germ.*

Type: *C. auricomum* Lindl.

Species: *C. auricomum* Lindl., *C. auricomiforme* Murr & Thell.

Chenopodium sect. **Vulvaria** (Standl.) Mosyakin & Iamónico, *comb. nov.*

Chenopodium [infragen. unranked] *Vulvariae* Standl., *N. Amer. Fl.* 21(1): 20 (1916).

Type: *C. vulvaria* L.

Species: *C. vulvaria* L. *s. lat.* (incl. *C. nidorosum* Otschiauri, *C. rhombicum* (Murr) F.Dvořák; probably also some other insufficiently known taxa; see discussion above).

Note: Following ICN Art. 21.2 and 32.2 (McNeill *et al.* 2012), the ending of the sectional name is changed as compared to that of the group name originally published by Standley (1916).

Concluding remarks

It can be thus assumed that the major diversity of Australian endemic taxa of *Chenopodium* (including *Rhagodia* and *Einadia*) was formed mainly as a result of one or a few dispersal events of Eurasian taxa from or *via* southeastern Asia (probably using coastal/littoral pathways), following one of scenarios outlined and generalised in Kadereit *et al.* (2005) for other Australian taxa of Chenopodiaceae. Judging from available data on morphology and biogeography, the link between sections *Acuminata* and *Auricoma* is probably explained by an independent migration event, so there were at least two independent cases of dispersal from Asia to Australia.

It is also noteworthy that the biogeographic and phylogenetic patterns observed in *Chenopodium* are very similar to some patterns revealed for Australian taxa of Camphorosmeae (Cabrera *et al.* 2009, 2011; Kadereit & Freitag 2011; Kadereit *et al.* 2014): a dispersal of some early-branching group followed by its explosive evolutionary radiation under conditions of the arid island continent characterised by extreme environmental conditions and potentially free ecological niches suitable for colonisation by the newcomers. It is indeed amazing that the whole great morphological diversity of Australian Camphorosmeae fitted into just one ‘*Sclerolaena* subclade’ sister to the Central Asian ‘*Bassia dasyphylla* subclade’; the latter is now recognised as the genus *Grubovia* Freitag & G.Kadereit, with just three currently accepted species (Kadereit & Freitag 2011).

There are also some biogeographic and taxonomic parallels with Australian Salicornioideae Ulbr. (see Shepherd *et al.* 2004; Shepherd *et al.* 2005; Piirainen *et al.* 2017), where several previously recognised and morphologically diverse Australian genera were subsumed under *Tecticornia* Hook.f. (Shepherd & Wilson 2007), similar to what has now happened to *Rhagodia* and *Einadia* subsumed under *Chenopodium*. In evolution of all these groups in Australia, long-distant dispersal or stepping stone migrations of a limited ancestral stock (probably via coastal habitats) and further explosive radiation were involved. The coastal migrational pathways seem to be especially evident in Salicornioideae, mainly because of the hygrophilic nature of the group.

The exceptional biogeographic, evolutionary and ecological role of littoral/coastal/alluvial habitats in shaping the desert floras and some of their ‘iconic’ taxa (including Chenopodiaceae) was especially well outlined by Iljin (1937, 1947, 1958; see also discussion in Kühn 1993; Mosyakin 2002, 2003b; Feodorova 2009, and references therein). Since then, Iljin’s concept (of which many Western researchers were fully unaware because it was published in Russian in little-known journals and serials) received solid confirmations from several molecular phylogenetic studies cited above. Similar ideas about the role of coastal/littoral habitats in the evolution of the Australian desert flora (including at least some representatives of Chenopodiaceae) were expressed by Burbidge (1960). Various opinions (sometimes conflicting ones) on Burbidge’s assertions were further discussed in many fundamental publications

on Australian plant geography (Barlow 1981; Carolin 1982; Parr-Smith 1982; Hill *et al.* 1999; Crisp *et al.* 1999 etc.; summarised by Murphy & Crayn 2017 and Ebach 2017).

For at least a few deviant taxa of Australian *Chenopodium*, different scenarios may exist. In particular, exceptional long-distance migration events from other directions (probably even from South America?) cannot be excluded as well (see case studies of long-distance migrations in Cain *et al.* 2000; Winkworth *et al.* 2002; Mosyakin *et al.* 2007; Stuessy *et al.* 2014, and references therein; Winkworth *et al.* 2015, and references therein). For example, possible relationships of *C. detestans* Kirk remain obscure. This species, known mainly from New Zealand (and reported as a rare and probably introduced plant in Australia), was often compared to *C. vulvaria*, partly because of its fetid odour and somewhat similar leaf shape, but Wilson (1983) suggested its affinity with mainly South American (extending northward to Mexico) *C. carnosulum* Moq. and *C. scabriculae* Speg. Considering the documented cases of long-distance dispersal between South America and New Zealand (Winkworth *et al.* 2002; Winkworth *et al.* 2015) and the rarity and possible non-native status of *C. detestans* in Australia, both these alternative scenarios should be considered and eventually tested by molecular approaches. We have seen too few specimens of *C. detestans* to make any morphology-based assumptions regarding its possible relationships.

Based on available evidence discussed above, we can make the following predictions and recommendations: (1) Most taxa of *Chenopodium s. str.* (including *Rhagodia* and *Einadia*) endemic to Australia and New Zealand are probably related to Eurasian taxa of the early-branching clade (or clades) within *Chenopodium s. str.*, forming together a clade (or a grade consisting of two to several clades?) sister to all other members of *Chenopodium*. (2) Any further dedicated molecular phylogenetic studies of Australian taxa of *Chenopodium* (those placed by various authors in sections *Auricoma*, *Desertorium*, *Polygonoidea*, *Rhagodioides*) should also involve not only Australian taxa earlier placed in *Rhagodia* and *Einadia*, but also, for comparison, the supposedly related Eurasian species, especially *C. vulvaria* (sect. *Vulvaria*), *C. frutescens* (currently unplaced in any section), and *C. acuminatum* and *C. vachellii* (sect. *Acuminata*). (3) To exclude (or, less probably, reveal?) some other scenarios of relationships and migration of some species, a comparative analysis of selected South American and some insular species, such as Hawaiian *C. oahuense* (Meyen) Aellen (= *C. sandwicheum* Moq.) and Juan Fernándezian taxa, would be desirable. Addition of *C. mucronatum* Thunb. may also be useful; however, judging from its morphology and biogeography, this southern African species is closer to other African taxa, such as *C. olukondae* (Murr) Murr and *C. ugandae* (Aellen) Aellen, related to *C. opulifolium* Schrad. ex W.D.J. Koch & Ziz. (the latter is presumably of Mediterranean–Central Asian origin, but evidently with African relatives). (4) As it stands now, the best taxonomic solution seems to be the inclusion of *Rhagodia* and *Einadia* in *Chenopodium*. (5) Infrageneric units (mainly sections) of *Chenopodium* will be most probably somewhat re-circumscribed to outline monophyletic groups within the genus, based on new molecular and morphological evidence.

Answers to the remaining intriguing questions of taxonomy, phylogeny and biogeography of Australian taxa of *Chenopodium* will be given by further molecular phylogenetic research. However, these phylogenetic studies should be accompanied by parallel morphological, biogeographical, ecological and other studies, and the voucher specimens sampled for molecular analysis should have reliable morphology-based identifications.

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